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16. ABSTRACT

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The purpose of AIRSILVA is to synthesize the best available knowledge on the effects of air pollutants on the mixed conifer forests of southern California, and to project potential ecosystem responses under alternative pollution scenarios.

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AIRSILVA: A MODEL OF MIXED CONIFER FOREST RESPONSE TO MULTIPLE STRESS[1]

Jeffrey Miller[2] and Lew Ladd[3]

Abstract. AIRSILVA is a model of mixed conifer forest community dynamics incorporating the population modeling capability of gap models and the mechanistic ecophysiology of process models to create a model where processes occur within individuals, and the failure of individuals to successfully complete processes results in population level dynamics.

The purpose of AIRSILVA is to synthesize the best available knowledge on the effects of air pollutants on the mixed conifer forests of southern California, and to project potential ecosystem responses under alternative pollution scenarios.

INTRODUCTION

Trees are notable for their long life-spans and large areas over which species or community types can be distributed. The scale of these organisms makes computer simulation modeling an important method for gaining insights into long-term community level responses of forests to multiple stresses. The stresses individual trees must deal with can be both natural, such as water or nutrient stress or man-caused such as ozone and acid-rain. But with the projected impacts of elevated CO_2, such as increased temperatures and corresponding water stress, these will be hard to separate.

Ecosystem functioning can be described at many levels of resolution. At each level of resolution there are certain appropriate phenomena of interest depending on the rates of the processes involved (O'Neill et al., 1986). Four time scales based on the cycles of nature are the diurnal (within a day), the seasonal (within a year), successional (within the disturbance frequency but without genetic change), and evolutionary (with genetic change). At the successional level the responses of forests to stresses usually focuses on species composition through time. Population models, such as gap models (Shugart, 1984) or vital attribute models (Noble and Slatyer, 1980) have been used to project the impacts of various stresses on the course of succession for many ecosystems around the world. Another view of succession concentrates on the changes in the rates and magnitudes of the processes which control the functioning of the ecosystem. Understanding these processes does not depend on knowing which individual within a species or within functionally similar species actually performs the functions.

AIRSILVA is a combination of the population modeling capability of gap models, and the mechanistic explanatory capability of process models. AIRSILVA is based on the gap model SILVA (Kercher and Axelrod, 1984a; 1984b) which is a version of the JABOWA model (Botkin et al., 1972) modified to simulate the mixed conifer forests of California and the roles of fire and SO_2 has on community composition. The modifications to SILVA replace the logistic growth function and rule-based growth constraining relationships found in most gap models with a simplistic set of ecophysiological functions that allows the effects of air pollutants to be incorporated with a degree of mechanistic realism. The reason for emphasizing the mechanisms of plant growth is that air pollutant stress is not an external phenomena but is part of the system and causes the plant to emphasize different growth strategies. By modifying the

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[2]Systems Ecologist, Corvallis, Oregon.

[3]Senior Programmer for NSI Technology, US EPA Environmental Research Laboratory, Corvallis, Oregon.

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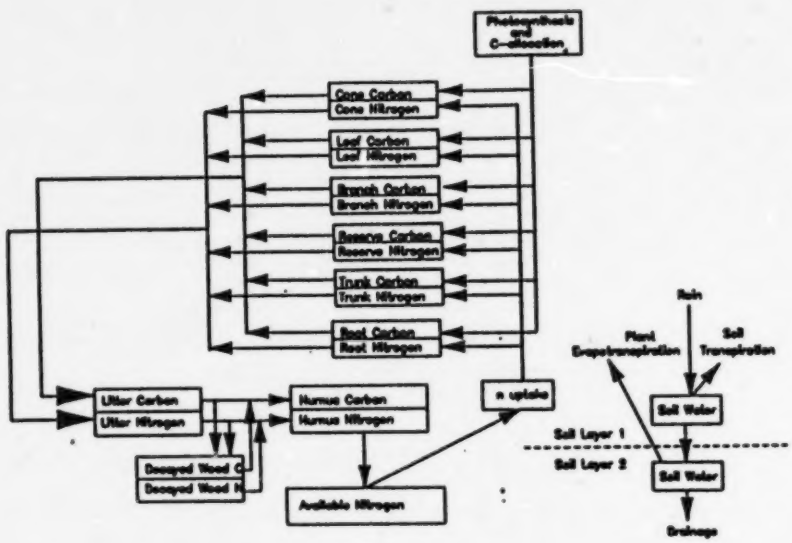

Figure 1. Each tree in AIRSILA has 5 carbon compartments; leaves of up to 5 age classes, branch, trunk, roots, and cones. There are 4 corresponding nitrogen compartments; leaves of up to 5 age classes, wood (incorporating both branches and the trunk), roots and cones. Carbon acquisition of each tree is a function of environmental conditions and the leaf area. Carbon allocation is based on the tree's desire to maintain an optimal carbon gain to nitrogen uptake ratio. Nitrogen uptake depends on the availability of nitrogen and the rooting volume. Nitrogen allocation at the community level is based on the relative demands of each individual tree and the decomposers. Nitrogen allocation within each tree depends on the relative sink strengths of each plant part. As litter ages it releases carbon and immobilizes nitrogen until it reaches a critical C/N ratio when it becomes humus and starts to release nitrogen as it continues to decompose.

patterns of allocation, as in increasing leaf area when the photosynthetic efficiency decreases, a plant may be able to compensate and show no decrease in annual growth rate.

AIRSILVA should project possible patterns of forest succession over long time periods, thus retaining the capabilities of a gap model, and also explain the observed pattern as the result of the underlying controlling processes. AIRSILVA is envisaged to be the longest time-scale model of a set of three hierarchical models. The other two models concentrate on the diurnal physiologicaly responses of a forest canopy to pollutants, and the seasonal ecophysiological response of a whole trees. The purpose of these models is to synthesize the available understanding concerning the effects of air pollutants, specifically ozone and acid-rain, on ponderosa pine and the mixed conifer forests of the southern Sierra Nevada and San Bernardino Mountains as a contribution of the Western Conifers Research Cooperative to the National Acid Precipitation Assessment Program.

ASSUMPTIONS OF THE MODEL

AIRSILVA follows other gap models and simulates the growth of individual trees on a plot (Shugart, 1984). The size of the plot is determined by the requirements of a single individual of the species requiring the largest amount of space. When this large individual dies it creates a gap in the forest canopy. This opening is usual-

ly invaded by many individuals of a fast growing light-requiring species. As these individuals grow they shade one another and eliminate the shorter individuals. A second growth pattern consists of species which may be slower growing, but are tolerant of shade. The shade tolerant species can grow under a closed canopy of the light requiring species, and once the light requiring species die come to dominate the stand. This successional cycle can then repeat once the shade tolerant species dies, creating another gap.

Gap models have the ability to mimic the hypothesized pattern of forest succession, but do not explain succession as a function of underlying processes. Birth and death are simulated as random events which can be biased with rules relating to the environmental conditions. Each run of a gap model is a single possible sequence of random events, and the models are usually run many times to develop a central response tendency of a forest.

In AIRSILVA the rules found in other gap models that directly link the environment to growth have been replaced with rules relating the environment to physiological functions. This allows population level responses to be explained as a result of the underlying physiological processes. This also allows the plant to have the ability to compensate for the environment. The effects of air pollutants may be so subtle that they only show up in the plants compensatory processes rather than its overall response.

Unlike other gap models where a continuous supply of seeds of all species is assumed, the soil seed banks in AIRSILVA depend upon the reproductive efforts of the individuals on the plot. This follows the logic of the vital attributes model which emphasizes the idea that species composition after a disturbance depends upon the species ability to survive the disturbance as either a resistant adult or as a seed.

Each individual tree is described by a set of carbon and nitrogen contents in various plant parts (Figure 1). Within the plot there is no explicit spatial arrangement of the individual trees. The leaf area of each tree is distributed vertically into layers, and is assumed that the leaves in each layer are spread over the whole plot. The roots of each individual occupy a fraction of the total soil volume. It is assumed that these roots are evenly mixed throughout the complete soil volume. This effectively means that within a plot the trees are growing under or above each other, but not next to each another.

The model increments tree growth once a year based on photosynthate accumulated on monthly time steps. The monthly time step is used to incorporate both the fluctuations in total annual rainfall and the seasonal pattern of rainfall which determines the length of the summer drought. Monthly carbon acquisition is calculated with an instantaneous gas exchange model driven by the average environmental conditions during the month. Acquired carbon and nitrogen are placed into reserve compartments, and the annual allocation pattern is a function of the reserve nitrogen to carbon ratio. A lack of nitrogen will increase allocation to roots, and a lack of carbon will increase allocation to leaves. Plant parts are assumed to maintain constant C/N ratios, so the total growth of all of the plant parts depends on the smaller of the two reserve pools.

Ozone is incorporated in the model as it is assumed to affect photosynthetic efficiency (Tingey and Taylor, 1982). Although acid rain has not be isolated as a major impact on western forests, AIRSILVA includes its possible effects on site nutritional balance, first as a supply of nitrogen and then as a detrimental soil acidifier as deposition rates increase.

AIRSILVA is written in C for portability between personal computers, work stations, and main frames. In C the FORTRAN or BASIC subroutines are called functions. One of the strengths of object oriented computer languages such as C is the ability to organize related information into data structures which are addressable with a single variable name. AIRSILVA has two main data structures, the "tree" and the "litter". Information on both the carbon and nitrogen masses of the parts of a tree, the exchange rates of these plant parts, as well as some general characteristics of the tree such as its height are arranged in a linked list of objects called "tree". Similarly, each years litter production is separated by material type and placed in a linked list containing information on its carbon and nitrogen mass, age, material type, etc. By using a linked list structure instead of an array, information does not have to be moved around in the computers memory; only a pointer to the location of the information needs to be updated. This data structure has greatly enhanced the computational speed of

Table 1. Information on each tree on the site is organized into a data structure called "tree". Of the thirty variables describing each tree the 12 parameters descride various properties of the tree, the 13 state variables describe the masses of carbon and nitrogen that comprise the tree and the accumulated ozone dose of each age class of leaves, and the 5 rate variables describe the transfer rates of carbon and nitrogen. Other information concerning each tree which does not need to be transferred between functions, such as the transpiration rate which is only used in the hydrology function, is not part of the "tree" structure.

Parameters:	tree number
	species code
	age
	annual growth ring width
	basal diameter
	height
	maximum branch mass attained
	crown thickness
	maximum crown thickness attained
	leaf area above canopy midpoint
	soil volume for water uptake
	soil volume for nitrogen uptake
State variables:	leaf mass (of up to 5 age classes)
	accumulated ozone dose (by leaf age class)
	carbon reserve mass
	branch mass
	trunk mass
	root mass
	new root mass
	cone mass
	leaf nitrogen content (by leaf age class)
	reserve nitrogen content
	wood (branch and trunk) nitrogen content
	root nitrogen content
	cone nitrogen content
Rate variables:	monthly average leaf conductance
	annual nitrogen uptake
	monthly net photosynthate (by leaf age class)
	annual wood respiration rate

AIRSILVA and allowed model development to proceed on personal computers.

The data structure "tree" describing each tree consists of 30 variables (Table 1). Twelve parameters describe which tree the individual is (tree_number), its species, age, annual ring width, basal diameter, height, the volume of soil available for exploitation of water and nitrogen, and three values used to determine the base of the crown. Thirteen state variables describe the carbon and nitrogen biomass compartments; leaf carbon and nitrogen (of up to five age classes), reserve carbon and nitrogen, branch carbon, trunk carbon, wood (both branch and trunk) nitrogen, root carbon and nitrogen, cone carbon and nitrogen, the new root carbon mass, and the accumulated ozone dose. Five rate variables; the leaf conductance, the net photosynthesis rate, the nitrogen uptake rate, and the wood and root respiration rates are also part of the tree structure since they are used in several functions and need to be related to a particular tree. All of the masses maintained in the model are in kilograms, and the distances are in meters.

The model is built in modules (C functions) that exchange information. Each function can be modified and improved or treated as a black box as needs vary, as long as the function performs the minimal tasks required of it by other parts of the model. Because the model includes numerous stochastic components it can be run several times and average responses determined, or the results of a single run can be analyzed.

AIRSILVA consists of 13 primary functions; init_stand(), init_output(), climate(), birth(), community(), hydrology(), c_up(), decomp(), n_up(), grow(), fire_(), kill(), and yearly_output() (Figure 2). The function init_stand() is called once at the beginning of each run to initialize the stand, and the other functions are then called once each year except for hydrology(), and c_up() which are called once a month.

```
main()
     {
     init_stand()
     for (year = 0 to number of years in run)
          {
          init_output()
          climate()
          birth()
               add_trees()
          community()
               get_leaf_area()
          for (month = 0 to 12)
               {
               hydrology()
               c_up()
               }
          decomp()
               newcohort()
          n_up()
          grow()
               carbon_alloc()
          fire_()
          kill()
          yearly_output()
          }
     }
```

Figure 2. AIRSILVA consists of 13 primary functions and has a one year time-step except for the hydrology() and c_up() functions which have monthly time-steps. The initial stand conditions are defined in init_stand(). Within the yearly loop climate for the year is generated in climate(), new trees emerge in birth(), and community() defines some general conditions on the plot. The plot water balance is calculated once a month in hydrology(), and the effect this has on carbon uptake is calculated in c_up(). Once a year decomp() determines the breakdown of organic matter and nitrogen availability for uptake in n_up(). The function grow() determines the growth of each tree on the plot based on the acquired carbon and nitrogen. Fires may occur and kill individuals in the fire_() functions, and then kill() removes trees that have died either due to an inadequate carbon gain for the year or as the result of fire. Finally the yearly_output() summarizes values on the water balance of the plot, the carbon and nitrogen cycling, and the population dynamics of each of the species on the plot.

Stand initialization

The init_stand() function defines the initial conditions of the stand at the beginning of each run. The model starts with "post fire" conditions; there are no trees, and no above ground accumulated litter. There is root litter, soil organic matter (humus), and corresponding nitrogen contents, and an initial seed bank of each of the species. The init_stand() function also calculates the total water storage capacity of the plot, which depends on the water holding capacity of the soil (l/m^3), the plot size and soil depth, and the rock content of the soil. The model starts with saturated soil water conditions.

The variables that summarize the conditions on the plot at the end of each year are initialized in the init_output() function. The output variables summarize four general areas; plot water balance, nitrogen cycling, carbon cycling, and population dynamics.

Climate

The climate() function corrects the monthly mean temperatures at the nearest weather station for the adiabatic lapse rate due to the elevation difference between the weather station and the plot being simulated. The number of degree-days over 5C are summed, and the monthly potential total solar radiation is corrected

for losses from clouds. The monthly mean and standard deviations for precipitation, ozone concentration, H^+, N, and S deposition are supplied to the model as required data. For each month of the year the climate() function generates values for these parameters from normal distributions.

Birth

The birth() and the add_trees() function that birth() calls add new individuals to the stand. If the annual degree day total is between the species specific minimum and maximum required for germination a fraction of the seeds in the soil germinate. The number of seeds that germinate is determined stochastically, with shade requiring and shade intolerant species having two different probability patterns as a function of the stand leaf area index (Figure 3). With increasing leaf area the shade intolerant trees have a decreasing probability of germination, and the shade requiring trees have an increasing probability of germination.

New seeds are added to the soil seed bank based on the reproductive efforts of the trees on the plot, and from off of the plot. This latter source prevents local extinctions of a species (as represented by either an adult or a seed) on the plot. Once the birth() function has calculated the number of new individuals of each species to be added to the plot, the initial masses of the seedlings and the other parameters maintained for each individual are defined in function add_trees(). Seeds lose viability and die following values reported for the model SILVA (Kercher and Axelrod, 1981).

Community totals

The community() function sorts the linked list of trees by height so the leaf area index above each individual can be calculated in the function get_leaf_area(). The leaf canopy of the community is divided into 25 layers from the top of the tallest tree to the ground. The leaf area in each layer is assumed to cover the whole plot. The leaf area of each individual is distributed vertically along its trunk from the crown base to the top of the tree following a normal distribution. The leaf area each individual contributes to the community canopy profile is summed. The leaf area above an individual consists of the leaf area in the canopy layers above the midpoint of the individuals canopy, and half of the leaf area of the layer at the midpoint. The light level at the midpoint of each individuals canopy is calculated following Beer's law (exponential decline). It is assumed that the leaves of each age class are equally distributed vertically, so all leaf classes experience the same light levels.

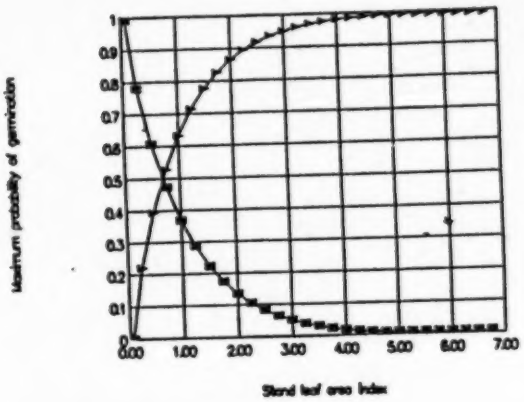

Figure 3. If the accumulated degree days at a site are within the species specific minimum and maximum tolerable then germination success depends on the species sensitivity to shade. Species are either shade requiring (●) or shade intolerant (■). The annual germination rate (seedlings/m^2) is a uniform random number up to the potenial maximum described by the light response function.

The community() function also determines the volume of soil that the roots of each tree can potentially exploit for water and nitrogen. The potential maximum volume of soil that the roots of the community can exploit for water is the sum of the volumes of each individual. These cylindrical volumes are calculated from the root mass of the individual converted to a length, and a radius around the root. Water uptake is assumed to occur along the complete root length. When the potential exploitable volume of the community exceeds the actual soil volume, each individual then exploits a fraction of the total soil volume equal to its volume divided by the community volume. Nitrogen uptake follows a two dimensional version of the same algorithm since it is assumed that the nitrogen dynamics take place at the surface of the soil. The nitrogen exploitable area is the rectangular area described by the root length and the exploitable distance from the root. As with the distribution of leaf area there is no spatial component in the distribution of each individuals roots in the community. All of the roots can explore the complete soil volume of the plot. The roots are

also not distributed vertically, but it may be more appropriate to distinguish two rooting zones, and have the trees either allocate to growth of surface roots for nitrogen uptake, or deeper roots for water uptake.

When the soil volume that could be exploited by the whole community is less than the total soil volume, the rate of nitrogen and water return to an individual limited by the carbon investment in roots. When the soil volume that could be exploited by the whole community is greater than the actual soil volume, the rate of return to an individual depends on its investment relative to all the other individuals. Since less than optimal C/N ratios within a tree will cause more investment into roots, this process of return related to investment simulates the individuals competing for nitrogen and water.

Plot hydrology

The plot water balance is calculated in the hydrology() function and the satvap() and penmon() functions which hydrology calls. During the one year time step of AIR-SILVA the hydrology() function is called once a month in order to capture both the variations in total annual rainfall, and the seasonal pattern of rainfall as it influences the summer drought.

On a monthly time step the random amount of rainfall generated in the climate() function is added to the top soil layer. If this new soil water content is greater than the water holding capacity of the layer then the excess is transferred to the second soil layer. If the second soil layer then contains more water than its holding capacity the excess is lost to drainage. The soil water contents of the two soil layers determine the soil water potentials of the two layers following a generalized soil water content to soil water potential function (Jeffrey, 1987). The water potential of the upper layer determines the soil surface conductance (Figure 4) which is then used in the Penman-Monteith equation (Monteith, 1973) to calculate actual soil evaporation.

It is assumed that the plants only extract water from the lower soil layer. The potential maximum water uptake is determined by the volume of soil exploited by the roots and the soil water content. The monthly average leaf conductances to water loss are based on the soil water potential, the monthly average light level, and the vapor pressure deficits following Jarvis (1976) as modified by Landsberg (1986). Actual transpiration is then calculated by the Penman-Monteith equation, but cannot exceed the potential maximum uptake. After soil evaporation has removed water from the upper soil layer, and the trees have removed water from the lower soil layer, there is vertical water movement based on a soil hydraulic conductivity value determined from the average of the water potentials of the two soil layers.

The soil is assumed to have a capacity to buffer H^+ deposition. If the accumulated deposition occurs faster than the soils ability to regenerate this buffering capacity the system will cross a threshold and nitrogen will begin to be leached from the soil. The rate of leaching is proportional to the available nitrogen and how far the soil buffering capacity has been pushed beyond the threshold.

Carbon acquisition

Along with the hydrology() function carbon acquisition and respiration costs are calculated in function c_up() once a month within the basic yearly time-step of the model. The average rate of photosynthesis for the month is calculated following Landsberg (1986) from the average leaf conductance determined in the hydrology() function, temperature, photosynthetically active radiation, external CO2 concentration, and the species specific potential maximum rate. This instantaneous rate is then multiplied by the day length and the number of days in the month. The photosyntheses equation incorporates leaf respiration, and the resulting net photosynthesis is calculated for each of the leaf age classes present on the tree. Leaf, wood, and root respiration rates depend on a base rate and a Q10 temperature function.

As leaves age the maximum photosynthetic rate decreases (Coyne and Bingham, 1982). Based on the field measurements of Coyne and Bingham (1981) the maximum rate of photosynthesis is assumed to decrease linearly with accumulated ozone dose. The ozone dose depends on the external concentrations and the leaf conductance. The maximum rate of photosynthesis also decreases linearly when leaf nitrogen contents are less than an assumed optimum. The production of photosynthate is assumed to require nitrogen. The carbon gain of all of the trees increases the plant nitrogen demand used

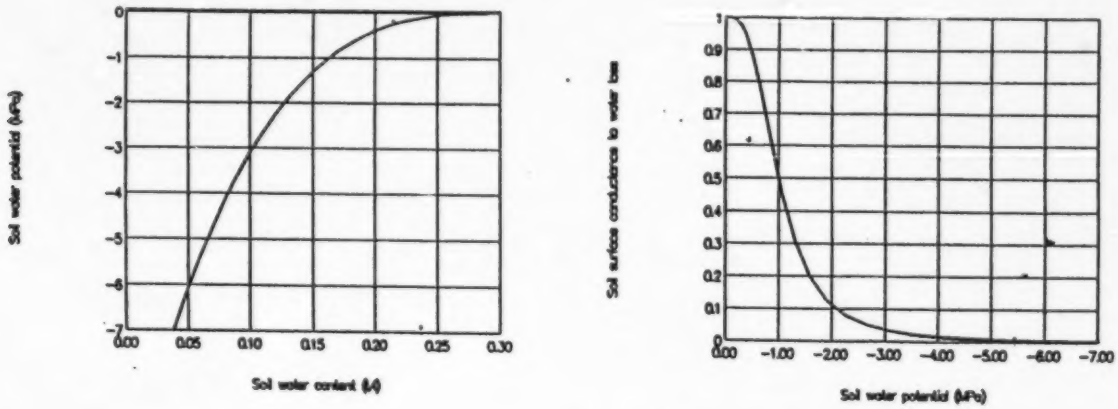

Figure 4. Soil water potential is calculated from a general relationship between soil water potential and soil water content (Jeffrey, 1987). The soil surface conductance to water loss is calculated from soil water potential based on a general function from Landsberg (1986). Both functions can be easily parameterized to fit soils of a specific site.

in the decomposition function to allocate nitrogen between the trees and the decomposition processes.

Decomposition

The decomp() function follows the decomposition routine developed by Pastor and Post (1985) in the gap model LINKAGES. Litter generated in the function grow() is of one of five materials; root, leaf, twig, small wood, or big wood. Each year a cohort of each class of material may be generated (as described in function grow()). Each of these cohorts is then placed in the linked list of cohorts and begins the decomposition process.

Each cohort of litter has a carbon and nitrogen content. Each year the material decomposes and releases carbon and immobilizes nitrogen until the material has reached a critical C/N ratio. These threshold C/N ratios vary depending on the type of material, and determine when the material is either transferred to the humus pool or the decayed wood pool in the case of the two classes of wood. Decayed wood continues to release carbon and immobilize nitrogen, but at a faster rate than the two types of wood litter. The humus also releases carbon, but in doing so releases nitrogen for either uptake by the plants or the decomposition process.

Because the decomposition of each cohort of litter and each tree is competing for the available nitrogen, a total demand is calculated based on how much nitrogen all of the trees need to satisfy their growth, and how much nitrogen each decomposing litter cohort could immobilize as it releases carbon. If this total demand is less than the available nitrogen then each cohort releases its complete amount of carbon, and immobilizes its complete amount of nitrogen. If the total demand is greater than the available nitrogen then the fraction of the available nitrogen each cohort can immobilize is proportional to its demand divided by the total demand. The amount of nitrogen immobilized then determines the amount of carbon released.

The potential rate of carbon release is presently a fixed fraction depending on litter material. The nitrogen that is immobilized in releasing this carbon depends on the litter material. Carbon release should be a function of evapotranspiration and litter lignin to nitrogen contents as in LINKAGES, if these regression equations can be developed for the litter in southern California. As in LINKAGES, humus releases 3.5% of its carbon and nitrogen each year, and as with the litter decomposition this should be made a function of the soil moisture availability and humus quality. Atmospherically deposited nitrogen is assumed to join the available nitrogen pool, and there is a fixed soil weathering rate adding nitrogen to the soil.

Nitrogen uptake

Nitrogen uptake by each individual tree is calculated in the function n_up(). The previous years growth in function grow() defined a demand for nitrogen by all of the trees. This years carbon acquisition increased the total plant demand. The fraction of this total demand which can be satisfied was decided in the decomp() function which divided the total available nitrogen between the trees as a group and the decomposition processes. Within function n_up() each tree receives a fraction of the nitrogen available to the trees. The amount of nitrogen an individual can take up is based on either the absolute volume of soil exploited, or the relative volume of the individual as a fraction of the complete community as described earlier.

Growth and allocation

The function grow() takes the nitrogen uptake values from the n_up() function and the carbon acquisition and respiration values from the c_up() function and calculates the net carbon available for growth. The function then calls the carbon_alloc() function which determines the allocation patterns for both carbon and nitrogen, and increments the plant masses (i.e. growth). If any of the plant parts are to be shed the grow() function also accumulates this years litter.

Each of the leaf age classes must be a net exporter of carbon, otherwise the age class is declared dead. Premature leaf death occurs when photosynthesis has been inhibited by exposure to ozone. Re-translocation of nitrogen and carbon out of a leaf class dying prematurely is not as efficient as when leaves die naturally. Each species has a maximum leaf life span, and the leaf class exceeding this age is transferred to leaf litter. Some of the nitrogen and carbon is re-translocated to the reserve compartments. Re-translocation is not completely efficient and a fraction of the nitrogen in the leaves becomes leaf litter nitrogen and most of the leaf carbon becomes leaf litter. The one year time-step of the model make realistic fine root turn-over difficult to simulate. In AIR-SILVA half of the root mass is defined to turn-over each year. This allows the fine root mass to not be completely dependant on each years allocation to roots and allows the mass to increase as the tree grow. Root nitrogen is re-translocated from the roots and a fraction is transferred to root litter nitrogen. Some of the root carbon is

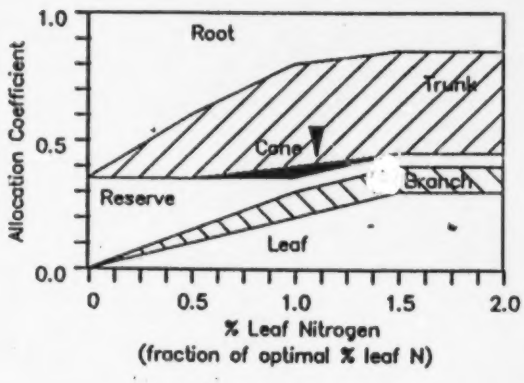

Figure 5. Allocation of carbon and nitrogen to the various plant parts depends on the ratio of reserve nitrogen to reserve carbon. The various plant parts have fixed nitrogen contents per unit carbon so the total amount of growth that can occur in a year is limited by the smaller of the two reserve supplies.Table 1. Information on each tree on the site is organized into a data structure called "tree". Of the thirty variable describing each tree the 12 parameters describe various properties of the tree, the 13 state variables describe the masses of carbon and nitrogen that comprise the tree and the accumulated ozone dose of each age class of leaves, and the 5 rate variables describe the transfer rates of carbon and nitrogen. Other information concerning each tree which does not need to be transferred between functions, such as the transpiration rate which is only used in the hydrology() function, is not part of the "tree" structure.

also re-translocated to reserves, and the rest becomes root litter. Branch shedding occurs when there is more branch mass than is needed to support the leaf mass. Branch shedding removes nitrogen from the wood nitrogen pool in relation to the amount of branch mass shed. No carbon is assumed to be returned when branches are shed. After the wood and root respiration costs have been satisfied, the net photosynthate is added to the reserve compartment. If the carbon reserves of a tree become negative then the tree is dead.

The allocation pattern for assigning carbon and nitrogen to leaves, reserve, branches, trunk, reproduction, and roots is a function of the reserve nitrogen to reserve carbon ratio (Figure 5). If the plant is light limited then the carbon reserves will decrease in relation to the nitrogen reserves. With high N:C ratios allocation shifts from roots and branches to leaves and trunk. If the N:C ratio decreases due to nitrogen limitations then allocation is shifted from the leaves, branches, and trunk to the roots.

The various plant parts are assumed to have constant nitrogen to carbon ratios, which define how much nitrogen is required to balance the allocation of carbon. If the required nitrogen is less than the reserve nitrogen then allocation uses all of the reserve carbon and as much of the nitrogen as is needed. If there is not enough nitrogen to satisfy all of the carbon allocation then allocation proceeds to the limit of the nitrogen supply. The allocation of carbon and nitrogen from the reserves back to the reserves allows the plant to maintain a supply to live on when conditions are less favorable.

Growth respiration and the cost of converting photosynthate into plant parts accounts for a fraction of the material allocated to each plant part. The model does not presently account for secondary leaf thickening, or allow partial death of any leaf age class.

When the cone carbon pool reaches 10 kg there is a reproduction event and the pool is set to zero. This event translates to a potential maximum number of viable seeds, depending on the cone nitrogen content. Less than an optimum C/N ratios cause fewer viable seeds. The 10 kg threshold value needs to be adjusted so that there is an appropriate periodicity in reproduction determined by the length of time it takes for the plant to accumulate sufficient reserves.

The basal diameter and height of the tree are calculated by turning the trunk mass into a cone shaped volume which has a species specific height to diameter ratio. The crown of the tree is initially distributed from the top of the tree to the ground. When the first branch shedding occurs a crown depth is defined as the height of the tree at that point. The branch mass is also recorded as the maximum branch mass. As the tree continues to grow the crown becomes a fraction of the total height of the tree equal to the crown depth. If the branch mass falls below the maximum branch mass the crown depth decreases. This allows AIRSILVA to simulate the observed pattern of ozone killing the lower branches and decreasing the crown ratio of ponderosa pine (Miller and McBride, 1988).

Fire

The set of fire_() functions calculate a probability of fire ignition, and then fire propagation based on the fuel load. Fires require sufficient litter load to ignite, and once burning, kill based on tree height and sensitivity to fire. The model views the linked list of trees organized by height as a fire ladder, and flames can jump up this ladder killing individuals until there is a step in height too large to jump. The size of the step that stops the fire ladder depends on moisture conditions, with drier conditions allowing the fire to jump larger steps. Sensitive species which have thin barks are killed whether or not their canopy is burned as in the model SILVA (Kercher and Axelrod, 1981).

Death

The function kill() removes individuals from the linked list of trees that have been tagged as DEAD in the function grow() or the function fire_(). When individuals die the leaf carbon and nitrogen contents are transferred to leaf litter as is the plant reserve carbon and nitrogen. The branches on the tree and the cones are transferred to the twig litter class and their nitrogen contents are transferred to the twig litter nitrogen pool. The trunks of the tree are either transferred to big wood or small wood litter depending on whether the trunk basal diameter was greater than 0.1m. Root carbon contents and nitrogen contents are transferred to root litter.

Annual summaries

The yearly_output() function generates output files on the nitrogen cycling, carbon cycling, plot hydrological balance, and the population dynamics of each species on the plot (Table 2). Individual trees can also be tracked in a fifth output file.

USES OF THE MODEL

AIRSILVA will be used to simulate three areas of ecosystem functioning; the hydrological balance, nitrogen cycling, and carbon cycling, and the effects these processes have on the species composition and size structure. The model will have the ability to investigate how these processes influence species succession, and how the shift in species composition influences the underlying ecosystem processes. AIRSILVA will be used to simulate the four broad areas; water balance, nitrogen cycling, carbon cycling, and population dynamics under natural conditions i.e. with "pre-man" fire frequency; with fire suppression; with the natural fire frequency and ozone; with the

Table 2. AIRSILVA generates output files concerning the annual hydrological balance of the plot, the nitrogen cycling, the carbon cycling, the number of individuals by 0.1 m increments in basal diameter of each species, and a file following one specific tree.

AIRSILVA annual output values

Water balance:	total rainfall
	soil drainage
	potential soil evaporation
	actual soil evaporation
	potential plant evapotranspiration
	actual plant evapotranspiration
	average soil water content (2 soil layers)
	average soil water potential (2 soil layers)
Nitrogen cycling:	potential nitrogen immobilization by decomposition
	actual nitrogen immobilization by decomposition
	potential plant uptake
	actual plant uptake
	mineralized
	total available
	leached
	leaf litter nitrogen content
	twig litter nitrogen content
	large woody debris nitrogen content
	small woody debris nitrogen content
	root litter nitrogen content
	decayed wood nitrogen content
	humus nitrogen content
	leaf nitrogen content by species
	reserve nitrogen content by species
	wood nitrogen content by species
	root nitrogen content by species
	cone nitrogen content by species
Carbon cycling:	leaf litter mass
	twig litter mass
	large woody debris mass
	small woody debris mass
	root litter mass
	decayed wood mass
	humus mass
	leaf mass by species
	reserve mass by species
	wood mass by species
	root mass by species
	cone mass by species
Population dynamics:	number of individuals by 0.1m increments in basal diameter by species
	number of viable seeds per m^2 by species
Single trees:	leaf mass (of up to 5 age classes)
	reserve carbon content
	branch mass
	trunk mass
	root mass
	new root mass
	cone mass
	leaf nitrogen contents (by age class)
	reserve nitrogen content
	wood nitrogen content
	root nitrogen content
	cone nitrogen content
	annual growth ring width
	basal diameter
	height
	leaf area index above the canopy midpoint

natural fire frequency and acid rain; and with actual conditions, i.e. fire suppression, ozone, and acid rain. The ecosystem responses to various future patterns of air pollutant emissions will also be investigated as part of the National Acid Precipitation Assessment Program.

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